

THREE NEW TIGER BEETLES of the  
GENUS *CICINDELA* from  
SOUTHWESTERN UNITED STATES  
(CICINDELIDAE-COLEOPTERA)

By

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Although most of the Southwest has been explored for tiger beetles, there is still an abundance of material that has remained either undiscovered or undescribed. The three tiger beetles subspecies described and discussed in this article are part of this material. They will be used to illustrate some of the interesting interdisciplinary correlations that can be achieved between entomology and geology, provided it is assumed that:

1. The rate of evolutionary change is very slow in tiger beetles, in some more so than in others. The resulting morphological changes have been minor, even in the more derived forms, so that these insects have remained relatively unspecialized for a very long time.

2. Environmental pressures forced many tiger beetle migrations along the ever changing hydrographic channels of various geological epochs of the Cenozoic era. This is the more evident in the arid Southwest.

The first assumption is based on comparison with *Carabid* fossils of Cenozoic age. Since no tiger beetle fossils have been recorded to date, it is assumed that their evolution paralleled that of closely related families, at least through this era. As for the second assumption, it is necessary for many species of these beetles to live close to water for ecological reasons; for example, the moisture content of the ground must remain between predictable limits for proper larval and pupal development. With the ecologies of many western species balanced on the proximity to permanent moisture, they must remain with watered places, or with moist areas with permanent subsurface water. The species that frequent lake shores and stream banks remain with their environment, even when the environment is moved, segmented, or re-formed for geological reasons. The Basin and Range Province which makes up much of the Southwest, contains many closed basins with disrupted, and often indistinct, hydrographic connections. These disconnected regions have served to isolate populations for extended lengths of time. Fortuitous dispersal of most of the riparian and littoral species of *Cicindela*, from one disrupted area to the next, does not take place easily, and from many observations, does not occur in fact.

Systematic studies of the regional physiography, grossly and in detail, indicate that some of the geological changes have had significant effects on tiger beetle evolution. Conversely, where tiger beetle change is observed, it is often possible to postulate the probable correlation between this change and the geological events. Hence, one can sometimes predict the occurrence of specific populations from the physiography, both past and present, and also, one can often reconstruct some of the geological changes from the random discovery of variant tiger beetle populations.

The sand dune tiger beetles are less predictable, maybe only because they require more study with regard to ecology, geological relationships, and overall distribution. Although the subspecies of *C. limbata* described herein is a sand dune dweller, an attempt will be made to correlate its derivation.

#### ACKNOWLEDGMENTS

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#### *Cicindela willistoni* estancia, new subspecies

Medium in size, narrow and convex, head and thorax bronze, elytra duller bronze basally, otherwise the white maculation is so confluent as to nearly cover the entire surface. Head and thorax as in ssp. *willistoni*, except that the proportions are narrower, and the sides of the pronotum are slightly more parallel. Elytra of male are narrower than in ssp. *willistoni*; the central basal area is pigmented only in the region below the scutellum, the maculation then converges abruptly toward the suture; the sutural ridge is pigmented throughout its length; a few minute bronze foveae form a line near the suture, diverging outward in the apical region. Underside bright blue, clothed with white decumbent hairs. Male—Length 11.7 mm, width 4.7 mm. Female similar to male but broader—Length 11.8 mm, width 5.1 mm.

Holotype male, allotype female, and 5 topotypical paratypes in the author's collection. Collected at the type location, 7.0 miles east of Willard, Torrance County, New Mexico, on 13 June 1959 (4 males including the type) and 28 September 1961 (1 male and 2 females).

Named for Pleistocene Lake Estancia.

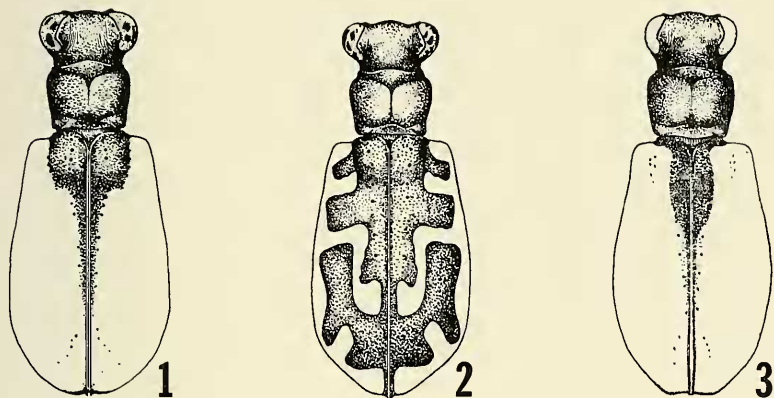


PLATE 44

Dorsal views. 1. *Cicindela willistoni estancia*, 2. *C. hirticollis corpuscula*,  
3. *C. limbata albissima*.

#### THE TYPE SERIES

The four male specimens that make up the June 1959 series are remarkably alike in form, size, and extent of maculation. One paratype is more dull and more green in color, while in two paratypes the sutural maculation is broader near the base, reaching barely to the row of minute foveae. All were caught in a draw leading to the open flats of a salt sink. This sink is one of many located east of Laguna del Perro and south of Laguna Salina, in the complex of basins that now forms the remnants of Pleistocene Lake Estancia. The area was covered by a layer of white alkali, and nurtured a sparse growth of short salt grasses. The ground was damp just below the leached out alkali cover. All specimens of the series were captured between the hours of eleven A.M. and noon. The weather was clear, with the temperature at 94°F.

The single male and two females captured in September 1961 are similar in maculation to the earlier specimens. The male is an old specimen, dull in color, with eroded pilosity particularly lacking on the frons. The females were teneral specimens, brightly colored, with full pile, but with elytral maculation still slightly greasy. The females, normally, would have hibernated, while the male died after a few days in captivity. They were caught between 10:30 A.M. and 1:00 P.M. at the edge of a playa that still contained water from Summer rains. The weather was clear but with a strong wind blowing from the southwest, while the temperature was at 70°F.

OTHER *CICINDELAE* WITH SSP. *ESTANCIA*

Three species of *Cicindela* were in evidence in June 1959. The *C. willistoni estancia* were flushed from the grasses of one small strip of ground, approximately 30 feet long by 8 feet wide. *C. fulgida* specimens were also flushed from grasses and clumps of grass, but over a much more extensive area. Individuals of *C. circumpecta johnsoni* were on the open flats, where the ground was smooth and damp. All specimens seen were captured so that the ratio of occurrence was, therefore, proportional to the number caught. The number caught is as follows: 4 *C. willistoni*, 14 *C. fulgida*, and 22 *C. circumpecta*.

In September 1961 there were five species of *Cicindela* at the edge of the playa. The number caught was as follows: 3 *C. willistoni*, 2 *C. fulgida*, 1 *C. punctulata*, 5 *C. togata*, and 1 *C. nigrocerulea*.

RELATIONSHIP OF SSP. *ESTANCIA* WITH OTHER  
SUBSPECIES OF *C. WILLISTONI*

Subspecies *estancia* is differentiated from all other subspecies of *C. willistoni* by an extreme amount of elytral maculation. This maculation covers about 74% of the total area of the elytra, whereas in ssp. *willistoni*, which is nearest to it in maculation coverage, this only amounts to between 40% and 50% of the total area. The maculation is reduced considerably in the more western subspecies, until it completely disappears in many specimens of ssp. *praeclata*. The color differences between subspecies also show much variation; in ssp. *estancia*, as in ssp. *willistoni*, it is generally bright reddish or greenish bronze, in ssp. *echo* it is usually brown, while in ssp. *pseudoscutilis* and ssp. *praeclata* it is dark blue green.

The discovery of a subspecies of *C. willistoni* in central New Mexico is significant by its isolation. The nearest populations are those of ssp. *willistoni* from the Laramie Plain of Wyoming, and ssp. *echo* from Little Salt Lake in southwestern Utah; both areas are 400 to 450 miles away. The Great Salt Lake populations of ssp. *echo* are about 500 miles distant, while the ssp. *praeclata* population at Lake Tecopa (dry) along the Amargosa River in Inyo County, California, is about 550 miles from Willard. There are no known intervening populations of this species. Significantly, *C. willistoni* has never been reported in any part of the Colorado River drainage system, hence none are found in Arizona, nor east of the Wasatch Mountains, from Utah through western Colorado.

The male genitalia of *C. willistoni* are distinct from all other tiger beetles by the unique design of the internal structures within the sac of the aedeagus. Representative internal sacs from all the subspecies were examined, both at rest and everted; in all cases the degree of variation is negligible. Small anomalies are due to



individual freedom of form within very narrow limits, while the main structural design pattern never varies. The form of the internal sac places this species in an intermediate position in the evolution of the more primitive nearctic *Cicindela*. The phylogenetic position lies between the *C. tranquebarica* complex (*C. tenuicincta*, *C. tranquebarica*, and *C. latesignata*) and *C. scnilis*, the latter being the more derived.

*C. willistoni* inhabits damp salt flats in areas of open drainage. It is very common in the Great Basin where it is always found on wet playas, i.e. playas with ground water at, or within a few inches of, the surface. It emerges late in the year, hibernates, then reappears very early in the following year, with elevation and latitude causing some readjustments in time.

### PHYSIOGRAPHY OF THE ESTANCIA VALLEY

The Estancia Valley lies near the geographic center of New Mexico, most of it south of the 35th parallel, and nearly bisected by the 106th meridian. It is east of Albuquerque, and south of Santa Fe. The valley lies to the east of the Manzano Mountains, which separate it from the valley of the Rio Grande River. The east of the valley is made up of hills that separate it from the uplands that extend to the Pecos River. To the north, the valley rises to a number of hills and mountains, while in the south the very distinct Mesa Jumanes encloses the region. The basin is one of internal drainage, consequently the central portion contains evidence of a pluvial lake known as Lake Estancia, described by Meinzer (1911), and Antevs (1935:308). According to both authors the lake covered, at its maximum, about 450 square miles; its surface was then at an elevation of 6,200 feet, and its maximum depth did not exceed 150 feet. The total drainage basin covers 2,000 square miles. Today, the lake bed is usually dry, except during the rainy season, or following heavy storms. The lowest parts are broken up into many sink-like depressions, except for the extensive north-south one called Laguna del Perro. These depressions are at ground water level, hence are classed as wet playas. They are sunken as a result of deflation caused by a prevailing southwesterly wind that has deposited the lake bed sands into low dunes on the east side of the valley. Wet playas, in the Southwest, always support some *Cicindela* life, and these, in particular, are remarkable for the large number of species supported.

### SPECIES OF *CICINDELA* IN ESTANCIA VALLEY

There are twelve species of *Cicindela* known to the author from Estancia Valley. Most of these were sampled east and southeast of Willard, a town on the southwestern side of the valley. They were found on the shores of sinks, in grasses near these sinks, or in grassland a great distance from the sinks. The best time for

collecting most of the tiger beetle species in the Southwest is after the rainy season starts. This season begins after July 1, and continues through September.

The littoral species:

1. *C. togata fascians* Casey, found on wet sands at the edge of water. July 1958.

2. *C. marutha* Dow, also near the water's edge, but not mixed with the above. These were scarce in July 1958.

The damp flat species:

3. *C. circumpecta johnsoni* Fitch, which were fairly numerous in July 1958, and June 1959. Of 37 specimens at hand, 24 are bronze, 11 are green, and 2 are blue. These are normal proportions for this subspecies according to Vaurie (1951:4).

4. *C. nevadica olmosa* Vaurie, found on the darker parts of the flats, but in relatively small numbers in July 1958. In these, the maculation is broad, as in typical ssp. *olmosa*, but the color is slightly more ruddy. This may be the upper limit of the range of this subspecies.

Species in grasses at the edge of playas:

5. *C. willistoni estancia* n. ssp., which by habit do not usually frequent these areas, but are usually seen in open spots, either near water, or far out on an alkali flat. It is probable that those specimens found here were young, had only recently emerged, and were about to descend to the open flats. This seems to be borne out by the fact that the four specimens of the type series are brightly colored, have all their setae intact, and show a lack of tarsal erosion.

6. *C. nigrocoerulea nigrocoerulea*  $\times$  *bowditchi*, these were all found at a mud hole on very wet ground at the edge of the grasses bordering the playa. This hybrid population contains admixtures of both parent populations.

7. *C. fulgida* Say, which were flushed from grasses, but alighted again among this sparse growth, not far from the edge of the playas.

Species on open roads or in sparse vegetation  
not over  $\frac{1}{4}$  mile from sinks:

8. *C. lemniscata rebaptisata* Vaurie, which is the subspecies with highly pigmented legs. The Estancia Valley is at the edge of the zone of hybridization between this subspecies and ssp. *lemniscata*. No hybridization can occur, however, because of natural mountain barriers to the west and south of the valley.

9. *C. punctulata chihuahuac* Bates. Of seven specimens captured, all were bright green to deep blue, except for one that had dark brown elytra with green foveae, as in typical ssp. *punctulata*.

10. *C. pusilla cinctipennis* LeConte. Only one broadly maculated specimen of this subspecies is available. It closely resembles Colorado members of the subspecies, although more samples are required to determine the true affinities of this population.

Species from open plains, found in grasslands far from water:

11. *C. flavopunctata rectilatera* Chaudoir, often found near water in the Southwest, hence this species must have a broad ecological tolerance. Specimens of *C. punctulata chihuahuae* were also found with these.

12. *C. obsoleta anita* Dow, the melanic form close to ssp. *santaclarae* is one of the largest nearctic tiger beetles, measuring about 20 mm in length. The sample from a few miles southeast of Willard was captured on 18 July 1958, at noon, when the temperature was 80°F., and the sky partly cloudy. The elevation above sea level was about 6,000 feet. Individuals were solitary, most of them hiding among the grasses, but when flushed, flew away slowly, but for a long distance. A few were mating. The sample specimens vary greatly in maculation, from totally immaculate, to those with full sets of dots as in typical ssp. *santaclarae*, or even with a complete marginal connection. This black form is found westward into Arizona, somewhat north of the locations where ssp. *santaclarae* is usually found.

#### CONCLUSIONS DRAWN FROM THE ESTANCIA VALLEY *CICINDELA* FAUNA

The Estancia Valley has been excluded hydrographically from other basins, at least during the pluvial periods of the Pleistocene; from this it may be concluded that migrations of *Cicindela* species, either in or out of the valley, have not occurred for at least the latter part of the Pleistocene, or roughly the past 100,000 years. Hydrographically, it is considered by Hubbs and Miller (1948: 117) to be a disrupted part of the Rio Grande System. The tiger beetle fauna indicates the following detailed hydrography:

1. The Estancia Valley was connected hydrographically to the Pecos River drainage system during the late Pleistocene. Half of the tiger beetle species of the valley belong, faunistically, to those of the Pecos region. These are *C. circumpecta johnsoni*, *C. nevadica olmosa*, *C. punctulata chihuahuae*, *C. flavopunctata rectilatera*, *C. lemniscata rebaptisata*, and *C. togata fascians*, all of which show no variation from those of the Pecos Valley, hence recent intrusion. The whole region, including Lake Encino, and several adjacent small areas of internal drainage, appears to be an embayment of the Pecos fauna, of recent origin. The Hills of Pederal, which separate the Estancia Valley from the eastern uplands, were formed by an uplift, according to Meinzer (1911:11), which probably happened in pre-pluvial times, but still during the late Pleistocene.

2. A connection between the Estancia Valley and the Tularosa Basin (Otero Drainage System) to the south is not evident. The only tiger beetles common to both basins are *C. nevadica olmosa* and *C. punctulata*, but these are also common to the Pecos fauna. *C. circumscripta johnsoni* has been replaced in the Tularosa Basin by its near relative *C. praeextata fulgoris* which appears to have a similar ecology, so that overlap is improbable between these two species. The Tularosa Basin specimens of *C. lemniscata* are hybrids, as this is the zone where ssp. *lemniscata* and ssp. *rebapicata* come in contact.

3. A connection between the Estancia Valley and a northern drainage system at some remote time is clearly evident. Several connections may have occurred to allow migrations of *C. fulgida*, *C. willistoni*, *C. nigrocoerulea*, and *C. obsoleta*. The peculiarities of the populations of these species, as they are found in Estancia Valley, point to a remote time.

*C. fulgida* is superficially different from northern New Mexico and midwestern populations by the broadening of the maculation, so that the lunules and bands are as confluent as in *C. parozana platti* of the Death Valley System of California. When more specimens of this population are examined, it may be discovered that this is a distinct subspecies.

*C. nigrocoerulea* is a hybrid between the southern populations of ssp. *nigrocoerulea* found from southwestern Texas to southern Arizona, and the southern Colorado populations of ssp. *bowditchi*. Of 24 specimens from Estancia Valley, only 7 are dark blue-black, while the majority are green; furthermore, they vary from immaculate to white-bordered as in typical ssp. *bowditchi*. It is postulated that ssp. *bowditchi* occupied the Estancia Valley region after mid-Cenozoic, and that its original range covered extensive areas to the east, and northward into Colorado. Long isolation during the Pleistocene produced the strong superficial difference between this subspecies and the nearly always immaculate ssp. *nigrocoerulea*. There was ample time for subspeciation, and later there was time also for isolation of a population in the area. The eventual intrusion of ssp. *nigrocoerulea* upon this isolated population of ssp. *bowditchi*, during the Pecos stage, caused the hybridization that is the mark of today's population.

*C. obsoleta* is very closely related morphologically to *C. nigrocoerulea*, but unlike the latter, it lives on dry, grass covered, uplands. Near Showlow, Arizona, there are similar melanic specimens at the same latitude, whereas at Springerville, Arizona, also at nearly the same latitude, typical ssp. *santaclarae* are found. Until more populations are discovered and examined, it will remain difficult to understand the derivations of this form.

## ORIGIN AND MIGRATION OF *C. WILLISTONI ESTANCIA*

*C. willistoni estancia* is most closely related to ssp. *willistoni* of the Laramie Plain of Wyoming. The chronological tracing of its ancestry can be hypothesized in a general way.

It was pointed out by Blackwelder (1909:430) that the Laramie Plain was a lowland at the close of the Cretaceous, and that through much of that epoch, the region was beneath the sea. At that time, the initial Rocky Mountain disturbance had not yet begun, so that the lowlands extended all the way to, and considerably beyond, the present site of Lake Estancia. It is probable that *C. willistoni* had not yet evolved into a species, but precursor species existed which were equipped with very rudimentary genitalic internal structures.

The orogenic Laramide Revolution, that marked the beginning of the Cenozoic era, caused important climatic changes affecting the ecologies of these early species, within the region of influence. The ancestral species began to take form in a region far to the north, so that the warmer, wetter, and subtropical Oligocene epoch had only partial effect on its development. Farther south, a whole host of new forms were evolved during this epoch; these were disseminated throughout the region, later migrated southward, and today form the bulk of the Mexican species.

Since *C. willistoni* was a more northern form, less affected by the period of greatest evolutionary pressure, it displays relatively lesser change. Following the warmer period, it spread across the whole mid-Cordilleran region to the Pacific Coast. In its eastern range it moved southward across the slowly rising, and drier lowlands, of Colorado and New Mexico, along intermittent saline flats characteristic of the drier Miocene. Renewed Rocky Mountain uplift, during this epoch, was not sufficient to interfere much with this species, except to create intermittent isolation around the extensive shallow lake system of that time. The great Pleistocene upthrust, however, completely isolated the population groups of Wyoming, New Mexico, and the Great Basin.

Only slight evolutionary change took place in *C. willistoni* after the period of formation. It is believed that this species came through the Miocene in its present form because from this epoch on, the general landscape was not severely altered, and the overall climate was relatively unchanged (it slowly continued to get drier), hence ecological pressure remained constant. It is the specific saline ecology of *C. willistoni*, coupled with fairly constant conditions that supported intermittent saline lakes in interconnected areas of internal drainage, that retained this species in its relatively unmodified state.



Subspeciation is a phenomenon generally associated with the Pleistocene, though in some species it may have begun during the Pliocene or earlier. Because of the recency of these epochs, widely separated subspecific populations are found which always retain their morphological identities with the phenotype, especially in the structures of the genitalia. To further uphold this condition, widely separated favorable habitats are still available, so that populations that have been separated for several hundreds of thousands of years are still extant. *C. zeillstoni estancia*, preserved by the favorable conditions in Estancia valley, is such a population.

### ***Cicindela hirticollis corpuscula*, new subspecies**

Medium to small in size, slender, dull bronze with broad complete maculation connected at margin. HEAD: Eyes prominent, interocular striae very shallow. Frons dimpled with many scattered pits from which arise white setae, these also extending to the sub-orbital region. Antennae bronze through the first four segments; scape with two setigerous punctures near the tip and forward of the junction with the second segment. Labrum white, the middle third extending forward into a flat protrusion, from the center of which arises a single, very small, sharp tooth. Mandibles white at base, with a bronze central band, and long acute black tips. Both sets of palpi pale in color, except for the last segment of each which is pigmented metallic green with a bronze cast; tips very slightly securiform. THORAX: Barely narrower than the eyes at its widest forward section, thence tapering so slightly toward the base as to appear nearly parallel. Disc bronze, median longitudinal impression shallow, while the anterior and posterior transverse impressions are deep. All impressions green at their deepest points. Posterior angles rounded, with a bulbous region between the posterior impression and the bottom edge. Sides of disc with long white hairs along the whole margin; a few recumbent hairs forward of the anterior transverse impression, with a bare spot at the center, also a very few hairs scattered over the lower half of the disc, blending into the side hairs. ELYTRA: Widest just forward of halfway, from there slightly narrowing to the apical third, where they curve inward evenly toward the suture. In the female the outer shape of the elytra differs from the male here described, in that the sides extend outward abruptly above the basal third, giving the female a broader appearance; the tip of the elytra is slightly recurved before reaching the basal spine. The ratio of length to width, in the type specimens, reflects this dimorphism, where the L/W ratio in the male is 2.43, while in the

female it is 2.29, indicating that the male is, indeed, relatively more narrow. Color bronze, pitted throughout the pigmented area, except for the sutural ridges which are unpitted and reddish bronze; pits green, numerous, and shallow, each with a slightly raised portion forward. Maculation white and relatively broad; humeral lunule with tip recurved inward and forward into a straight line ending in a small bulb. Apical lunule with a slightly recurved tip. Middle band entering from the side in a forward line nearly parallel to the extension of the humeral lunule, thence descending into a deep, longitudinal apical extension, with sinuous contour on the sutural side; it terminates with an inwardly directed bulb that nearly reaches the sutural ridge. The side margin is complete, broad above the middle band, then tapering narrowly, but very slightly, to the humeral lunule; broadens steadily to more than halfway to the apical lunule where it smoothly narrows nearly to the vanishing point before connecting to the latter, this narrow section is slightly more extensive than the width of the inner extension of the apical lunule. UNDERSIDE: Color metallic blue-green in the middle, bronze at the head and thoracic sides. Head: Genae bright bronze with fine deep striae, color becomes greenish near the eyes. Gula dull bronze and glabrous. THORAX: Episterna coppery, and bearing long white recumbent hairs. Sterna shining green and glabrous, except for the metasterna which have bronze areas, with long white hairs, covering nearly half the region adjacent to the metaepisterna. Anterior and median coxae green and glabrous, but for the region adjacent to the metaepimera, which are covered with hairs. Abdomen: Bright green with blue reflections. Outer half of sternites moderately covered with short recumbent hairs. Penultimate sternite of the male has a shallow penial notch, lying to the left of the body centerline, to accommodate the asymmetrical penis. Legs: Trochanters dark, with green reflections, glabrous. Legs covered with the usual hairs and bristles; bright reddish bronze, femora tinged with green near the connection with the tibia; tarsal joints long, the combined tarsal joints of the male longer than the anterior tibia; tarsal claws moderately long, rear ones nearly  $2/3$  the length of the fifth tarsal segment. DIMENSIONS: Male — Length 11.3 mm, width 4.7 mm. Female — Length 11.7 mm, width 5.1 mm.

Holotype male, allotype female, and 20 topotypical paratypes from Potholes, Imperial County, California, collected 12 May 1946. 35 paratypes collected on the banks of the Colorado River as follows: 3 from 14 miles south of Needles, San Bernardino County, California, 10 May 1952; 2 from Imperial Dam, Yuma

County, Arizona, 16 April 1954; 8 from Yuma, Arizona, (2 by F. H. Shoemaker, 1904; 2 from the Blaisdell collection, 1922; and 4 by E. P. Van Duzee, April 1923), and 22 from Moab, Grand County, Utah, 23 July 1959 (M. C. Slagle), 2 paratypes from Gila Valley, Graham County, Arizona, 14 September 1924 (D. K. Duncan), 2 paratypes from Phoenix, Arizona, no dates, and 1 paratype from St. George, Washington County, Utah, no date, (V. M. Tanner).

The name is from the latin *corpuscula* meaning small body.

### DISTRIBUTION OF TYPICAL SPECIMENS

Holotype, allotype, 25 paratopotypes and 7 paratypes in the author's collection. 2 paratopotypes in the U. S. National Museum, Washington, D.C., in the care of Dr. O. A. Cartwright. 12 paratypes in the collection of the California Academy of Sciences, San Francisco, California, in the care of Mr. Hugh B. Leech. 16 paratypes from Moab, Utah, in the collection of Mr. M. C. Slagle of Ft. Lauderdale, Florida.

### THE TYPE SERIES

The type series of *C. hirticollis corpuscula* consists of 64 specimens. The main characteristics of the series are the smallness of size, and the relatively wide maculation, especially in those from the lower Colorado River Basin. The series may be divided into two distinct population groups: 1. The lower populations, found along the Colorado River below Grand Canyon, especially from below Needles, to the Gulf of California, and also along the main tributaries, i.e. the Virgin, and the Gila — Salt Rivers. 2. the upper population, recorded from Moab, Utah, well above the Grand Canyon.

Measurements substantiate this smallness in size, as shown in Table A. The two population groups of ssp. *corpuscula* were compared to each other, as well as to a Pacific Coast sample of *C. hirticollis gravida*.

Table A  
Comparison of Length in Various Populations  
of *C. hirticollis corpuscula*, and *gravid*

subspecies	population	sample size		longest	shortest	average length		standard deviation
		n	♂	♀		$\bar{X}$	$\bar{X} \delta \quad \bar{X} \phi$	
corpuscula	Lower Colorado	27	12	15	12.4 ♀	10.0 ♂ ♀	11.3      11.0      11.5	.50
	Upper Colorado	22	8	14	13.0 ♀	11.2 ♂	12.1      11.7      12.5	.58
gravid	Pacific Coast	30	15	15	14.5 ♀	12.0 ♂	13.3      12.8      13.7	.57

COMPARISON OF SSP. *CORPUSCULA* WITH  
OTHER SUBSPECIES OF *C. HIRTICOLLIS*

Subspecies *corpuscula* may be differentiated from all other subspecies of *C. hirticollis* principally by the small size, and wide maculation. *C. hirticollis ponderosa* is also broadly maculated, but is much larger in size—in his original description, Thomson (1859:23) lists it between 13 and 15 mm—and its range is the southern Midwest, and along the Gulf of Mexico from Texas to Vera Cruz, Mexico, although Harris (1911:15, in footnote), questioned the propriety of all but the Mexican population from near Vera Cruz, and possibly the Arizonian specimens. Cazier (1954:241) reported ssp. *ponderosa* from Algodones, Baja California, Mexico (near Yuma, Arizona); these cannot be in consonance with the larger size of ssp. *ponderosa*, and therefore are referred to ssp. *corpuscula*. *C. hirticollis graxida* of the Pacific Coast is also larger, but with narrow maculation and a greenish color. *C. hirticollis abrupta* is also larger, darker, and with very distinctly and abruptly narrowed elytra at the apical third, especially in the female. *C. hirticollis shermani* is a doubtful race that is blackish bronze in color, with sharp elytral apices, and though relatively small, according to Casey (1916:30) it is still larger in size (12.5 mm), but narrower (4.6 mm).

The lower Colorado River population of ssp. *corpuscula* is reddish bronze in March and April, the color turning to a darker dull bronze by June and July. This population is of the more typical form, and is well developed throughout most of the lower Colorado River Basin. Some small specimens, very similar to this subspecies, have been noted from Texas.

The upper Colorado River population from Moab is intermediate in size, with a maculation that is more in keeping with, but less variable than typical ssp. *hirticollis*. It is more closely related to the lower Colorado River populations of ssp. *corpuscula* than to other subspecies, primarily because of the smaller size, and the geographical location along the Colorado River. This population has been known for some time, having been reported by Tanner (1929:80). The population along the lower Colorado River has been known for still longer, the first report coming from Wickham (1899:220) who stated that H. C. Fall took it along the river during July; later, Tanner (1929:80) recorded it from St. George, Utah, along the banks of the Virgin River.

*C. hirticollis corpuscula* is a gregarious riparian subspecies throughout its range.



RELATIONSHIP OF SSP. *CORPUSCULA* WITH  
ITS GEOGRAPHICAL LOCATION

The theory originally advanced by Blackwelder (1934: 560) on the origin of the Colorado River states, in brief, that during the late Pliocene, the Rocky Mountains of Colorado were lower, maybe as low as 5,000 feet, so as to allow the westerly winds to carry their moisture beyond the range, thereby causing the formation of a semi-arid region westward. Since the Colorado uplift had not yet begun, he further states that in that time there existed a region lower in altitude, and distinctly more arid than now, and that this landscape extended from Wyoming, Utah, and Colorado, south into Mexico. Consequently the Colorado River was small, had reached grade or nearly so, and entered the Gulf of California on the eastern side since the latter extended considerably into the region now occupied by the Mojave and Colorado deserts. With the Pleistocene uplift, the mountains of Colorado provoked more rain and the river grew, enabling it, by volume, to maintain itself at the same general grade. This is the uplift theory that explains meanders in deeply encised gorges, such as the Goosenecks of the tributary San Juan River, near Mexican Hat, Utah.

One of the first effects of uplift was the formation of a series of lakes along the path of the river. This was the beginning of isolation for the tiger beetle populations. Later, by adjusting itself to a more direct path, the river filled and overflowed these lakes, then created deep gorges. By then, populations were not only isolated, but the chance of intermingling from time to time became less and less possible, until deepening gorges, such as the Grand Canyon, became such imposing barriers as to cause complete isolation of the populations from up and down the river. It has been advanced that the Colorado River has been cutting its way through a gradual uplift for nearly a million years. It may be assumed that the riparian tiger beetle populations were isolated for some lesser part of that time, so that something in the order of 300,000 years will be the best guess for complete isolation of the upper and lower population of *C. hirticollis corpuscula*.

In the nearly 300,000 years of total isolation there were no evolutionary pressures of any consequence on these two populations. Under the conditions, any evolutionary change brought on by isolation would be restricted to size, color, or maculation coverage. Any change in morphology would not be noticeable because *C. hirticollis* belongs to one of the most primitive groups of the nearctic *Cicindelae*; this is indicated by most rudimentary structures in the internal sac of the male armature.

While the upper Colorado River population somewhat recalls small ssp. *hirticollis*, the lower Colorado River and tributary populations are still smaller, more distinctly marked, and possibly more reddish bronze in color. These modifications indicate an origin based on several widespread migrations of the ancestral species. There was a possible migration into the Colorado Basin from the north after mid-Cenozoic. Another migration, of a more widely maculated relative to ssp. *ponderosa*, may have entered the basin from the east or southeast during the same period. Migrations were stopped from reaching the Pacific Coast by the extension of the Gulf of California. Migration, in and out of the basin, may have continued until late Pliocene.

It is believed that the mixing of these ancient stocks created the basic pattern for ssp. *corpuscula* which then evolved during the long isolation that followed. It is this very genetic derivation that brought about variations between the upper and lower Colorado River groups following this isolation during the latter half of the Pleistocene. A basic plasticity was retained that caused the one population to partially converge to the appearance of the northern migrants, while the other converged in appearance to the eastern migrants; each reverting to the preponderant genetic force of its region, albeit both are still small in size, but unequally so.

The Little Colorado River enters the Colorado River at the eastern end of Grand Canyon, below Marble Canyon, in a region isolated from both the upper and lower populations of ssp. *corpuscula*. In the upper reaches of this tributary, at Holbrook, Arizona, there is a very distinctive, large, red, and broadly maculated *C. hirticollis* of considerably different origin. It is foreign to the Colorado River populations.

#### GEOLOGICAL AND FAUNAL CONCLUSIONS DRAWN FROM SSP. *CORPUSCULA*

1. *C. hirticollis* entered the Colorado River Basin by two routes, one from the north, the other from the east. It developed characteristics of subspecific nature during late Pliocene or early Pleistocene.

2. Isolation of populations by the great canyons at midriver created an upper river population at Moab, Utah, slightly distinct from the lower river population. The Virgin and Gila river drainage systems have been connected to the lower Colorado River system, at least since early uplift time.

3. The Little Colorado River was created during, and as a result of uplift. Prior to this, its upper basin was part of an eastern hydrographic system.

*Cicindela limbata albissima*, new subspecies

Medium to small in size, narrow, convex; head and thorax green, elytra almost completely covered with white maculation. HEAD: Bright green with a bronze central tinge between the eyes, extending from the vertex to the occiput, in an area that is granulately wrinkled; interocular striae fine and tinged with blue, especially behind the eyes; clypeus bright green with a bright blue suture; frons punctate, from each puncture arises an erect white hair; hairs on head numerous and erect, covering the frons, vertex, and the entire area between the eyes; the eyes are not excessively prominent; first four joints of the antennae are bronze, the third and fourth joints with a more metallic red tint, scape with 3 or 4 hairs forward of, and above the junction with the second joint; labrum white and truncate, feebly curved anteriorly, and with a very small central tooth, submarginal hairs 8 to 10 in number; mandibles long, white at their basal  $2/3$ , terminating in sharp black tips; joints of palpi pale testaceous, but not the last ones which are pigmented and with tips slightly securiform. THORAX: Pronotum narrower than the eyes, subquadrate, widest forward, thence tapering very slightly to the base; surface granulately wrinkled; long hairs covering the sides, and halfway to the longitudinal impression; this impression is very shallow, while the transverse impressions are deep: ELYTRA: Wider at the shoulder than the head, then tapering outward slightly for nearly  $2/3$  their length, at which point the body reaches maximum width; from there the elytra are smoothly rounded to the apex; in the latter half of this curve, the edge is micro-serrulate; the apical tooth is barely indicated. The pigmentation of the elytra is dull bronze, consisting of a small area at the humeral disc nearly parallel to the suture; this area begins at the green scutellum, it is about  $1/3$  the width of the elytra, broadens slightly for a distance equal to its width, then tapers toward the suture for nearly  $2/3$  the length of the elytra; the sutural ridge is brightly pigmented throughout its length; the sutural bronze foveae nearly parallel the suture, then extend outward  $3/4$  of the way to the apex; the rest of the elytra is dull white but for two short rows of black foveae near the outer edge of the humeral disc; the entire white surface is covered with widely separated micro punctures, these punctures are raised forward in the central apical region in an indistinct band. UNDERSIDE: Bright green with bluish tinge centrally, also blue where there are impressions; covered nearly throughout with long white decumbent hairs; genae wrinkled and hairy; sides of thorax hairy laterally; front and median coxae hairy, back ones bare on top but not so laterally; center of abdomen nearly bare except for a few hairs at the edge of the segments; penial notch of moderate depth but off-center with respect to the centerline of the body, bearing to the left side to accommodate the

asymmetrical penis; legs are a bright green, bearing a medium amount of white hairs and bristles; the tarsal joints are of medium length, and bear a number of white recumbent hairs; the tarsal claws are very long, the rear ones are fully as long as the last tarsal joint.

The female is similar to the male except for being a little broader in the elytra, and being slightly larger in size. DIMENSIONS: Male—Length 10.8 mm, width 4.4 mm. Female—Length 11.7 mm, width 4.7 mm.

Holotype male, allotype female, and 115 topotypical paratypes from Coral Pink Sand Dunes, located 14 miles south of Mt. Carmel Junction, Kane County, Utah. Elevation 6,300 feet. Collected at the following dates: 9 on 5-6 August 1958 (E. R. Tinkham), 40 on 17 September 1960, and 68 on 29 September 1960, this last date includes the type specimens.

Name from the latin *alba* (white) and the superlative *issima*, hence, very white.

#### DISTRIBUTION OF TYPICAL SPECIMENS

Holotype and allotype in the author's collection. Paratopotypes as follows: 5 to Dr. E. R. Tinkham of Indio, California; 5 to Dr. M. A. Cazier, Director, Southwestern Research Station of the American Museum of Natural History, Portal, Arizona; 5 to the California Academy of Sciences in the care of Mr. Hugh B. Leech; 4 to Dr. O. A. Cartwright of the United States National Museum, Washington, D.C., 2 to Dr. H. Howden of the Canadian Department of Agriculture, Ottawa, Ontario; 2 to Dr. F. Truxal of the Los Angeles County Museum, Los Angeles, California; 2 to the Reverend B. Rotger C. R. of Pagosa Springs, Colorado; 2 to Dr. J. A. Knudsen of Pacific Lutheran University, Tacoma, Washington; 2 to Dr. F. M. Beer of Oregon State College, Corvallis, Oregon; 2 to Dr. W. A. Drew of Oklahoma State University, Stillwater, Oklahoma, and the balance of 84 in the author's collection.

#### THE TYPE SERIES

This whole series is homogeneous with few exceptions. In some specimens the color is closer to blue, while the pigmentation is nearly all green and the legs are a greenish blue. In others, the central apical irregular areas of the elytra have a few faintly pigmented dots in close juxtaposition, in the region that is normally pigmented in other subspecies. *C. limbata albissima* is the only member of its species found west of the Continental Divide, considerably to the west of the Rocky Mountains. It may be readily distinguished from ssp. *limbata* and ssp. *nympha*, of the midwestern United States and Canada, by its lack of discal pigmentation

in the apical region of the elytra, and from ssp. *hyperborea* of Canada's Northwest Territories and northern Alberta which is darkly pigmented, and maculated in the more conventional *Cicindela* fashion.

## BIOLOGY AND ALLIED SPECIES

*C. limbata albissima* is a sand dune tiger beetle. On the Coral Pink Sand Dunes, individuals of this subspecies emerge suddenly on the northern side of dunes, between the hours of 9:30 and 10:00 A.M., first by the few, then increasing in numbers, but always remaining solitary. Those collected in September were teneral specimens, only recently emerged, as borne out by their softness of body, especially in the earlier sample, also the bright pigment, the full pilosity, and the fact that the sexes were about evenly divided. Of the 40 collected on 17 September 1960, there were 19 males and 21 females. Two weeks later, 66 were captured, of which 32 were males and 34 females. The 9 specimens collected in August of 1958, by Dr. Tinkham, were old specimens with well worn claws from long exposure to the motion of the sand, also with a darker, mat pigmentation, which is also an indication of advancing age. It is evident that this population emerges in September and October, then hibernates until Spring; the last specimens disappear in August, or just prior to the emergence of the new generation.

Since none were mating, it was of interest to find out if this was by choice or necessity. From an inspection of several male armatures, it was discovered that this organ had not yet hardened, and at the time, was unsuited for mating. Mating probably begins after Spring emergence, and it is unlikely that any overlap of the generations results in intermating.

On the early September visit, there was evidence that it had rained heavily the day before from the large rain spots on the sand. When the upper layer of the sand had dried in the 80°F. temperature, the insects began to appear. On the 29th of September there was an increasing southwesterly wind that rippled the sand surface, until it reached 15 knots at noon; so much sand was stirred up by that time, that the few tiger beetles remaining out sought shelter on the lee side of the slightest rise, finally, even these few insects failed to appear. The early morning coolness of the sand may have something to do with the late appearance of these insects. As the temperature increased they became wary, until it was extremely difficult to approach them on the open sand without their taking flight. Their burrows were somewhere on the lee side of very large dunes, in sandy areas covered by scattered brush, as the beetles flew that way when disturbed. Those not disturbed were seen alighting on the steep sides of dunes, then fly-



ing up and over the top, to sun themselves on the more exposed sand.

The sand of the Coral Pink Sand Dunes is very fine in texture, and will saltate in the slightest breeze at the level of the tiger beetles. It is this fine blown sand that causes erosion of their hairs and tarsal claws. Because of the wind conditions associated with sand dunes, these active insects will seek shelter when the velocity is too high for controlled flight; this may be a reason for finding them more numerous at the edge of the dune area, especially on the downwind side. The Coral Pink Sand Dunes cover several square miles, and are situated on the windward side of a range of hills called the Vermilion Cliffs. Their direction is southwest to northeast, along the line of prevailing winds. The composition of the sand is finely ground sandstone, of Chinle formation. These were the only species of *Cicindelids* found in the dunes.

The subspecies of *C. limbata* inhabit sandy areas, and preferably sand dunes. This is the strongest ecological characteristic of the species. Species allied to it morphologically have similar ecologies; these include *C. thecatina* Rotger of the Great Sand Dunes in the San Luis Valley of south central Colorado, and *C. bellissima* Fall of the sand dunes found along the Oregon-Washington coast, and the Columbia River Valley. The subspecies of *C. limbata* live at intermediate elevations, up to 6,300 feet, *C. thecatina* at 7,500 to 8,000 feet, while *C. bellissima* is found at, or near, sea level. It is not the elevation, nor the proximity or isolation from water, that is the characteristic of their combined ecologies, but rather their affinity for sandy habitats. Because of this they exhibit a wide tolerance of latitude and faunal zones.

*C. limbata*, the easternmost species of this complex except for ssp. *albissima*, displays variations in maculation with latitude; this is equivalent to change in elevation at the same latitude, so let us examine it from this standpoint. The more extensive pigmentation prevails, on this basis, at the higher elevations (equivalent to more northern latitude); this is exemplified by ssp. *hyperborea* of northern Canada. The lack of pigmentation shows up at lowest elevation (lower latitude equivalence), as represented, in the extreme, by ssp. *albissima*. This may have something to do with the amount of reflection or absorption of light that they will tolerate, then again it may only be a coincidence resulting from other factors. To be considered is the probability that during the glacial periods of the Pleistocene, ssp. *hyperborea* migrated northward ahead of the Keewatin Advance, while the more northern Canadian populations of ssp. *nympha* and ssp. *limbata* were forced to lower latitudes. Following glaciation, ssp. *hyperborea* returned southward, while during the latter part of the Pleistocene ssp. *albissima* gained altitude

(northern latitude equivalence). This may explain the greater pigmentation of ssp. *hyperborea* on the basis of longer isolation from the main population groups, at a very northern latitude. Conversely, the lack of elytral pigmentation in ssp. *albissima* may be due to longer isolation also, but at more southern latitudes. If latitude actually does control the amount of elytral maculation in this species, then it might be expected that in the future ssp. *hyperborea* will lose some pigment, while ssp. *albissima* will gain pigment.

## ORIGIN AND MIGRATION OF

### *C. LIMBATA ALBISSIMA*

A branch of *C. limbata* moved freely in and out of the Colorado River Basin during the mid-Cenozoic (Miocene) by a migration route across Wyoming, Montana, and Alberta via the Green River Basin and other basins farther north. This route was available until early Pleistocene. If this hypothesis is correct, then ssp. *albissima* is more closely related to the Canadian ssp. *nympha* than to ssp. *limbata*. To further support this view, it is noted that *C. formosa* and *C. scutellaris*, both closely related to each other, both near related to *C. limbata*, and both ecologically tolerant of sandy locations, are found together in sand blowouts near the Yampa River, a short distance from Maybell, Colorado. This *C. formosa* is ssp. *gibsoni*, identical to the typical form of Saskatchewan, while the *C. scutellaris* is an endemic form, closely related to ssp. *criddlei* of Manitoba.

Since *C. limbata* and *C. hirticollis* have a similar type of genitalia, and therefore belong to the same phylogenetic group, it is postulated that, although the two species are distinct ecologically, they were derived somewhat on the same time scale. This strengthens the earlier conclusion that there was a migration route for *C. hirticollis* into the Colorado River Basin from the north. The method of migration chosen by *C. limbata* was of necessity quite different from that chosen by *C. hirticollis*.

It is concluded that *C. limbata* was a relatively northern rudimentary nearctic species at the beginning of the Cenozoic. It remained in the north, and it developed without influence from the Rocky Mountain uplift. Because of this, it was not under pressure to alter its basic habits, thus enabling it to remain unspecialized to this day. The intrusion into the Cordilleran region was along a natural migratory route, at a time when climatic conditions were favorable. These favorable conditions have not totally changed, hence ssp. *albissima* is able to survive in the Colorado River Basin, although very restricted in its distribution.

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|------------------------------------|-----------------------------------|
| ▲ <i>C. limbata limbata</i>        | ⊕ <i>C. willistoni willistoni</i> |
| ▲ <i>C. limbata albissima</i>      | ○ <i>C. willistoni echo</i>       |
| ■ <i>C. hirticollis corpuscula</i> | ● <i>C. willistoni estancia</i>   |

## PLATE 45

Map of a portion of southwestern United States showing location of some tiger beetle populations of the genus *Cicindela*.